

EVOLUTIONARY AND NEWTONIAN FORCES

CHRISTOPHER HITCHCOCK

*Division of Humanities and Social Sciences
California Institute of Technology*

JOEL D. VELASCO

*Department of Philosophy
Texas Tech University*

A number of recent papers have criticized what they call the *dynamical interpretation* of evolutionary theory found in Elliott Sober's *The Nature of Selection*. Sober argues that we can think of evolutionary theory as a theory of forces analogous to Newtonian mechanics. These critics argue that there are several important disanalogies between evolutionary and Newtonian forces: Unlike evolutionary forces, Newtonian forces can be considered in isolation, they have source laws, they compose causally in a straightforward way, and they are intermediate causes in causal chains. Here we defend and extend the forces analogy by arguing that each of these criticisms is based on a misunderstanding of Newtonian forces. Our discussion also has the interesting consequence that natural selection turns out to be more similar to forces such as friction and elastic forces rather than the more *canonical* gravitation.

1. Introduction

A number of authors, including notably Elliott Sober in *The Nature of Selection* (1984), have argued that the theory of evolution can be usefully understood as a theory of forces similar to Newtonian mechanics. Newtonian forces act to alter the positions and momenta of material bodies whereas evolutionary forces such as natural selection, drift, mutation, and migration act to change gene frequencies in populations. We will follow Walsh, Lewens, and Ariew (2002) in referring to this conception of evolutionary theory as the *dynamical interpretation*.¹

Contact: Christopher Hitchcock <cricky@its.caltech.edu>

Contact: Joel D. Velasco <joel@joelvelasco.net>

1. We will use *dynamical interpretation* to refer specifically to those that understand natural selection, drift, mutation, and migration as forces. As an anonymous referee pointed out, some philosophers conceive of these as causes, while regarding the analogy with Newtonian forces as inapt.

Recently, several philosophers have criticized the dynamical view, offering instead what they call *the statistical interpretation* of evolutionary theory. Representative papers include Walsh (2000); Walsh, Lewens, and Ariew (2002); Matthen and Ariew (2002); and Matthen and Ariew (2009). One of the foci of their critique has been the analogy between Newtonian and evolutionary forces.

This critique has drawn a number of responses, and the debate has been wide-ranging. Nonetheless, we believe that we have a new type of contribution to make. Defenders of the statistical interpretation claim that evolutionary theory lacks certain features essential to a dynamical-forces view and defenders of the dynamical view have responded by arguing that evolutionary theory does indeed have these features, or at least something sufficiently close to count as appropriately analogous. However, in our view, much of this dialectic rests on false presuppositions about what a theory of forces must look like. Newtonian mechanics does not even exhibit the features in question. Since Newtonian mechanics is *the* exemplar of a theory of forces, if it lacks the relevant features, then obviously they are not necessary conditions for a dynamical theory of forces.

Examining the analogy between evolutionary theory and Newtonian mechanics is important for a number of reasons. First, it tells us something about the logical structure of evolutionary theory (as well as Newtonian mechanics). In particular, it tells us about the way in which information about selection, drift, migration, and mutation is used to construct a mathematical model describing the evolution of gene frequencies in a population. Second, the analogy bears on the causal status of evolutionary forces such as natural selection, drift, migration, and mutation. Forces in Newtonian mechanics, such as gravitational forces, electro-magnetic forces, friction, and elastic forces are usually taken to be *causes* of motion. If an argument purports to show that natural selection is not a cause of evolutionary change because it has certain properties, that argument is substantially undermined if, say, friction has the same properties. Moreover, Maudlin (2004) argues that causal notions emerge when we have a theory that is “quasi-Newtonian.” The success of the analogy between Newtonian mechanics and evolutionary biology bears directly on whether the latter has a quasi-Newtonian structure.

Finally, our discussion sheds light on the nature of analogy in science. Tim Lewens, a sometime defender of the statistical interpretation of evolutionary theory, writes: “Are drift and selection forces? It is best not to phrase the question as bluntly as this. Instead, one should simply ask in what respects drift and selection resemble Newtonian forces, and in what ways they differ, paying attention all the time to the dangers of a seductive metaphor” (Lewens 2010: 316). We agree. In particular, we will argue that both evolutionary forces and Newtonian forces are heterogeneous. Thus, to say only that evolutionary forces are analogous to Newtonian forces is a comparatively uninformative claim. If asked to name a kind of force in Newtonian mechanics, most of us would think first of gravitation, and

then perhaps of electrostatic forces. We will call these the *canonical* Newtonian forces. We do not mean this term to describe anything about the ontological or metaphysical status of these forces. By *canonical*, we mean only that these are likely to be the first forces one would name if asked to give an example of a force in Newtonian mechanics. Other kinds of forces, such as those due to friction and springs, seem less important, and are less celebrated additions to the Newtonian framework. Likewise, one might think of natural selection as the exemplar of an evolutionary force, while mutation and migration are likely to be afterthoughts. We will argue, however, that gravitation and electrostatic forces are more closely analogous to mutation and migration, while natural selection behaves more like friction or springs. So there is a sense in which the canonical forces within each theory are disanalogous. There is a kind of mismatch in which the paradigmatic forces of one theory are matched up with the less heralded forces of the other.

While the debate between the defenders of the dynamical and statistical interpretations of evolutionary biology has been the primary locus of discussion of the forces analogy, our concern in the present paper is with the analogy for its own sake. We hope to defend, extend, and clarify the analogy. The debate between proponents of the dynamical and statistical interpretations extends to issues well beyond the aptness of the analogy, and we will not directly address these further issues. Moreover, while we take the upshot of our analysis to be generally favorable toward the dynamical interpretation, we are happy if defenders of the statistical interpretation wish to adapt some part of our analysis for their own purposes.

One point of terminology: We will use the expression *evolutionary forces* to denote factors like natural selection, drift, mutation, and migration, which defenders of the dynamical view have *claimed* to be analogous to forces in Newtonian mechanics. We do not intend the expression, by itself, to imply that evolutionary forces really are forces in something like the sense of Newtonian mechanics. We hope, by the end of the paper, to convince the reader that the label is apt, but we do not mean to presuppose it from the beginning. Despite the potential to mislead, we will mostly avoid using scare quotes, *so-called*, and other hedging devices when talking of evolutionary forces in an effort to enhance legibility.

2. The Dynamical View

Before examining criticisms of the dynamical view, it is important to understand exactly what this view is. There is no single dynamical view of evolution any more than there is a single statistical view. Different proponents of the dynamical view develop their positions in interestingly different ways. Even Sober's views have changed over time. Nonetheless, the central criticisms we examine can all be traced back to Sober's characterization of evolution as a theory of forces (Sober 1984),

so we will begin there. Sober (1984) describes one of the goals of a theory of evolution to be a description of the range of possible causes of evolution. Evolution here is taken to be a change in the gene frequencies of a population, as is standard, though Sober is careful to say that this is merely a rule of thumb and not a hard-and-fast principle (Sober 1984: 30). He then says:

All possible causes of evolution may be characterized in terms of their “biasing effects.” Selection may transform gene frequencies, but so may mutation and migration. And just as each possible evolutionary force may be described in terms of its impact on gene frequencies, so it is possible for a cause of evolution to be present without producing changes in gene frequencies. . . . All this is to locate evolutionary theory in familiar territory: it is a theory of forces. (Sober 1984: 31)

Sober goes on to describe what he means by a theory of forces. He takes such a theory to consist of a zero-force law, which says what happens to a system when no forces act on it, source laws, which describe the circumstances that produce forces, and consequence laws, which describe how forces, once they exist, produce changes in the system. These laws should include singleton force models, which say what each force achieves when acting alone, as well as compositional laws about how to combine forces.

Sober’s own view takes the Hardy-Weinberg Law to be the zero-force law for evolutionary theory. This is not essential; Brandon (2006) and McShea and Brandon (2010) accept the forces analogy but claim that the appropriate zero-force law is the ZFEL (the zero-force evolutionary law), in which an absence of forces leads to increased diversity and complexity. Here, rather than engage in this dispute, we simply note that there are at least some strong reasons to prefer thinking of drift as an agent of change. (Stephens 2010; Barrett et al. 2012). For our expository purposes, we will take the Hardy-Weinberg law to describe the zero-force condition, thereby treating drift as a force. Though not universal, this is certainly a standard presentation in evolution and population genetics textbooks.

One formulation of the Hardy-Weinberg Law (or principle or model) is as follows:

If a population exists with two alleles, A_1 and A_2 , with frequencies p and q respectively, then in a single generation the population will settle into genic and genotypic equilibrium with gene frequencies p and q , and genotypic frequencies of $A_1A_1 = p^2$, $A_1A_2 = 2pq$, and $A_2A_2 = q^2$ —provided that there is no selection, mutation, migration, nonrandom mating, or drift.

A population with these genotype proportions is referred to as being in the Hardy-Weinberg equilibrium, and by repeated applications of this law, we can see that,

barring the introduction of any evolutionary forces, the population will remain at these proportions in evolutionary stasis.

Various kinds of generalizations of the Hardy-Weinberg law are easy to derive—for example, what happens when there are more than two alleles at a locus or when we are interested in genotypes with multiple loci. But the key feature is the same: We achieve stasis barring the introduction of any forces. Much of population genetics theory deals with asking what happens when we relax various assumptions built into this law. For example, the Hardy-Weinberg law assumes there is no mutation. But what if there is? Mutation can cause a change in gene frequencies in a population and, as such, it is an evolutionary force. As a simple example, imagine that the mutation rate from A_1 to A_2 is μ while the back mutation rate is negligible. Then if we start at the Hardy-Weinberg equilibrium, after one generation the frequency of A_1 will become $p' = p - \mu p$ while $q' = q + \mu p$. After n generations, the frequency of A_1 will be $p_n = p_0 \times e^{-\mu n}$.²

The Hardy-Weinberg law also assumes that there is no selection. But what if there is? No problem. Assign the relative fitnesses of the genotypes as follows: $A_1A_1 = w_{11}$, $A_1A_2 = w_{12}$, $A_2A_2 = w_{22}$. Then the genotypes will contribute to the next generation in the ratio: $p^2 \times w_{11} : 2pq \times w_{12} : q^2 \times w_{22}$. To find the actual frequencies, we normalize by dividing each value by the average fitness. Similar simple adjustments to the Hardy-Weinberg ratios can be made for various kinds of assortative mating, migration, and drift. But what if there are multiple forces at work? Here we need consequence laws, which tell us how to add the results of various forces. Luckily, population geneticists are quite clever and they have derived many such results—often helpfully contained in chapters with titles such as “Interactions of Natural Selection with other Evolutionary Forces” (Templeton 2006) or “Diffusion Theory: Combining Evolutionary Mechanisms” (Rice 2004). Many of these results are quite advanced, but some are quite simple. For example, we can combine our results above to find out what will happen to a population under selection with mutations present. Stephens (2004: 554) uses just such an example from Ridley (1996: 115–116) in order to provide further evidence that we can think of evolutionary forces as having magnitudes and directions [with notation variants]:

Ridley . . . describes a simple case where there is genetic variation at a locus with two alleles, A and a . Suppose further that there is selection against the dominant allele (A), so that the fitnesses of the three genotypes AA , Aa and aa are $(1 - s)$, $(1 - s)$ and 1 , respectively. Imagine further that mutation opposes selection. Let μ = probability that a mutates into A . What will the equilibrium frequency (p^*) of A be in this case? Here $p^* = \mu / s$. Since

2. To derive this, think of the generation time as infinitesimally short. Then we can say that in each generation, $\Delta p = dp/dg = -\mu p$. So $(1/p)dp = -\mu dg$. Integrate both sides from p_0 to p_n and 0 to n then solve for p_n .

mutation rates are generally small (typically, $\mu \approx 10^{-6}$ or 10^{-7}), even a modest selection pressure of $s = .01$ means that the equilibrium frequency of A will be very small. Notice the sense in which there is a *direction* to the force of mutation, and notice how (in this case) it *opposes* selection. We can also talk about cases where the force of mutation *more or less strongly* opposes selection, and cases where mutation operates in the *same direction* as selection.

Stephens's example is a special case of the basic result that in the *mutation-selection balance* the equilibrium frequency of the mutant allele a is $q^* = \mu/[hs + q^*s(1 - h)]$ where h is a measure of dominance (so that when $h=1$, a is dominant as in Stephens's example). This is usually simplified to $q^* \approx \mu/hs$. For a completely recessive allele, $h=0$ and so $q^* = \sqrt{\mu/s}$.

This result is no mere mathematical curiosity. For example, Morton, Crow, and Muller (1956) use these results together with empirical studies of the results of inbreeding in humans to estimate the number of lethal, recessive mutations we all carry in heterozygote form. From this, they can estimate mutation rates in humans. More generally, these results are important to evolutionary theory since they help explain the maintenance of genetic variation of all kinds in populations through time.

One might object that these results cannot be valid in real, finite populations due to random effects that are especially important when such small frequencies play an essential role. True enough. Rice (2004) chapter 5 shows how to extend this case to include the expected effects of genetic drift. Even for population sizes of 10,000 (and especially for smaller effective population sizes) the results are noticeably different from the infinite case. Here, the allele is expected to be missing in many populations and above the equilibrium frequency at many others. These results are also of great theoretical interest. Motoo Kimura (1968) famously posited the *neutral theory of molecular evolution*, in which he argued that the dominant factor in molecular evolution was random, neutral mutations that get fixed by genetic drift. In a series of papers, Kimura, Tomoko Ohta, and others generalized this to the *nearly neutral theory* in which many mutations that have slightly deleterious (or later, advantageous) effects can also go to fixation (see Ohta and Gillespie 1996 for a historical overview). These and related results are central to modern evolutionary theory, and they depend essentially on combining the forces of selection, mutation, and drift.

In response to Stephens's example above (and another from Brandon and Ramsey 2007), Matthen and Ariew (2009) argue that these results are not relevant since these are in no way analogous to the Newtonian paradigm of adding forces by vector addition. While it is not clear in what sense (if any) evolutionary forces are additive, what matters to Sober's presentation is that the theory has some way

of combining them with consequence laws. This is called the *compositional problem*. There is no particular reason to think that we cannot combine forces just because we cannot simply add up their effects as if they were independent.

A theory must discover how to combine the forces it describes. . . . Newtonian mechanics has made vector addition a familiar paradigm for computing the net effect of forces acting in concert. But it is only one example, and other more complex interactions are certainly possible. . . . Each theory of forces must solve this compositional problem for itself, there being no antecedent recipe that is guaranteed to work for all cases. (Sober 1984: 31–32)

While Sober says that this difference does not undermine the forces analogy, one might be tempted to think that this is a deeper problem than Sober admits. We will examine the compositional problem and Matthen and Ariew's arguments about it later in the paper.

The above examples should be sufficient to get the gist of what Sober means by thinking of evolutionary theory as a theory of forces. But is this appropriately analogous to Newtonian mechanics?

3. The Statistical View

Beginning around 2000, several philosophers, most prominently André Ariew, Tim Lewens, Mohan Matthen, and Denis Walsh, began to develop an alternative picture of evolutionary theory, which has been labeled the statistical interpretation. Defenders of the statistical view maintain that evolutionary forces such as selection, drift, migration and mutation are not *causes* of evolutionary change. Matthen and Ariew (2002: 56) suggest, in lieu of the analogy with Newtonian forces, an analogy with the *estimated rate of return* on an investment. This estimated rate is not a cause of the appreciation of an investment; it is just a prediction of how the investment will grow in response to the economic factors (whatever they may be) that are genuine causes of growth. Another analogy might be with life expectancy.³ Life expectancy is not a cause of longevity; it is simply an estimate of longevity. Defenders of the statistical view think that evolutionary forces are more like estimated rate of return or life expectancy than like Newtonian forces.

The debate between proponents of the dynamical interpretation and the statistical interpretation has many moving parts. In the course of the debate, defenders of the statistical interpretation have made a number of claims, including:

3. Sober (1984: 95) makes this analogy.

1. The analogy between Newtonian forces and evolutionary “forces” such as natural selection, drift, mutation, and migration is misleading. (Walsh 2000; Walsh, Lewens, and Ariew 2002; Matthen and Ariew 2002; Matthen and Ariew 2009)
2. The quantitative parameters that appear in evolutionary models, such as fitness coefficients, do not describe causes of evolutionary change, but rather the probabilistic expectation of such change. (Matthen and Ariew 2002: 56–57, 67–68)
3. The Hardy-Weinberg law is not a true *zero force* law. For example, it does not apply to asexual reproduction. (Matthen and Ariew 2002; also mentioned in Matthen and Ariew 2009 but not defended there)
4. It makes no sense to ask what would happen if natural selection were acting “alone.” It is always acting in some kind of material substrate (e.g., genetic inheritance via diploid sexual reproduction). (Matthen and Ariew 2002)
5. Evolutionary forces do not obey an additive law, like Newtonian forces. (Walsh, Lewens, and Ariew 2002; Matthen and Ariew 2002; Matthen and Ariew 2009)
6. It is impossible to look at the change in a population over one or more generations and decompose it into the part caused by natural selection, the part caused by drift, etc. (Walsh, Lewens, and Ariew 2002; Matthen and Ariew 2002)
7. It is a category mistake to call natural selection a “cause” of evolutionary change. This reifies natural selection. The causes of evolutionary change are things like predation, sunlight, and competition, or variation with respect to cold resistance in a particular population of beetles.⁴ (Walsh 2000; Walsh, Lewens, and Ariew 2002; Matthen and Ariew 2009)
8. Natural selection may be a probabilistic cause in some sense, but it is not a causal process in the sense of Salmon (1984) or Dowe (2000). It is not a fundamental process. (Walsh 2000; Matthen and Ariew 2002)
9. Natural selection is an effect of adaptation (or better, of adaptability) rather than vice versa. (Walsh 2000)
10. There is no distinction between evolution and natural selection. (Matthen and Ariew 2002)
11. Natural selection supervenes upon individual outcomes (e.g., births, deaths, matings). (Walsh 2000; Walsh, Lewens, and Ariew 2002; Matthen and Ariew 2002; Matthen and Ariew 2009)

4. The allusion is to an example presented by Millstein (2006) and discussed by Matthen and Ariew (2009). See below for further discussion of this example.

12. Natural selection is a mathematical truth, rather than an empirical truth. (Matthen and Ariew 2002; Matthen and Ariew 2009)
13. Natural selection is just a statistical aggregate over causal processes at the individual level. (Walsh 2000; Matthen and Ariew 2002; Matthen and Ariew 2009)
14. Natural selection is a statistical artifact, rather than a genuine event, akin to the motion of the center of mass of an N particle system when one of the particles is accelerated. (Walsh 2000; Walsh, Lewens, and Ariew 2002; Matthen and Ariew 2009)
15. Natural selection is best understood by a *hierarchical realization model* (Matthen and Ariew 2002; Matthen and Ariew 2009)

Some of these claims are intended to provide support for others, but it is not clear that one is forced to accept or reject all of these claims together as a suite. They are not equivalent. It is not even clear that they are consistent. It is also unclear whether any one proponent of the statistical view would accept all of these claims.

The challenge to the dynamical interpretation has sparked a lively and interesting debate. Defenders of the dynamic view have been forced to clarify their positions in a number of ways, and several distinct variants of the dynamical interpretation have emerged. A number of authors have disputed some of the claims above, a small collection of which includes Rosenberg and Bouchard (2005), Abrams (2007), and Brandon and Ramsey (2007), who focus on their treatment of fitness, selection, and drift; Reisman and Forber (2004), Millstein (2006), and Shapiro and Sober (2007), who focus on causation; Stephens (2004), Brandon (2006), and Filler (2009), who explicitly defend the forces analogy; and Sober (2011), who addresses the claim that natural selection is just an analytic truth.

Examining all of these claims in a single article would be impossible. Our focus in the present paper is claim (1), which challenges the analogy between evolutionary and Newtonian forces. We construe (2) through (6) as claims intended to undermine the analogy and will examine them in greater detail as well. We will largely be defending the analogy, so our analysis is likely to be favorable to the dynamical interpretation. However, it is not our intention to defend the dynamical interpretation in whole. If defenders of the statistical interpretation wish to use some aspect of our analysis to defend some part of their position, we invite them to do so. (We will mention one such possibility in the next section.) Our goal is only to clarify the analogy; we will leave it to the proponents of the two interpretations to elaborate on the role of the clarified analogy in the larger dialectic.

Defenders of the statistical interpretation have focused primarily on natural selection and genetic drift, saying relatively little about other evolutionary forces

such as migration and mutation. While we will discuss natural selection at some length, we have relatively little to say about drift. Drift is the evolutionary force that looks least like a Newtonian force to us. By contrast, we will argue that the analogy is particularly strong for migration and mutation. In this respect, the version of the analogy that we will defend is not perfectly aligned with the version that defenders of the statistical view have attacked. Perhaps then, this part of our analysis will do little harm to the statistical position. That is fine with us, since our primary concern is with clarifying the analogy.

We will focus our discussion on the two papers by Matthen and Ariew (2002; 2009). Matthen and Ariew are more explicit than any of the authors on either side of the debate in what they take a theory of forces to require. They also examine the analogy with Newtonian forces more closely than anyone else. It has now been more than a decade since the publication of Matthen and Ariew (2002), and numerous publications have appeared on both sides of the debate (of which we have mentioned only a few). To our knowledge, no one on either side of the debate has challenged the picture of Newtonian forces that is painted by Matthen and Ariew. In doing so ourselves, we thus take ourselves to be challenging presuppositions that have been at least tacitly accepted by both sides of the debate.

4. Analogies

Mary Hesse (1966) provides a familiar framework for thinking about analogies in science. An analogy involves a *target* system, which we are trying to understand, and a *model* system. In our present topic, the target system is evolutionary biology, and the model system is Newtonian mechanics. In any such analogy, there is a *positive analogy*, *negative analogy*, and *neutral analogy*. The positive analogy involves those features of the two systems that are known to be analogous. The negative analogy involves those features that are known to be disanalogous. The neutral analogy involves those features where it is not known whether they are analogous or not. The neutral analogy is thus the domain in which we hope to acquire new knowledge of the target system by extending the analogy.

As Stephens (2004) notes, the analogy between evolutionary theory and Newtonian mechanics was never intended to be perfect. And there are important points of disanalogy. For one example, there is no evolutionary analogue of Newton's third law. Consider the case discussed by Millstein (2006) involving populations of montane willow leaf beetles in different parts of California. The relative prevalence of the PGI-1 and PGI-4 alleles varies across these populations. The research of Rank and Dalhoff (2002) suggests that beetles that are homozygous for the PGI-1 allele have greater resistance to cold temperatures than those that are homozygous

for the PGI-4 allele (with heterozygotes having an intermediate level of resistance). If the cold climate creates a selection pressure favoring the PGI-1 allele in a population of beetles, the beetles do not exert any opposing force on the climate.⁵

A more important disanalogy results from the stochastic nature of evolutionary change. Evolutionary forces can determine the expected representation of alleles or phenotypic traits in the next generation, but there will be chance deviations from this expected value due to sampling error. There is no obvious analogue of this in Newtonian mechanics. Brownian motion is perhaps the closest analogue.⁶

⁷ One certainly can combine deterministic forces with Brownian motion. For instance, particles suspended in a fluid might be subject to gravity and Brownian motion, and we can combine these to predict the vertical distribution of particles. But Brownian motion does not result from sampling error and is not dependent on the size of a population. For this reason, we think that there are important conceptual issues concerning the role of chance, the status of drift, and how to combine drift with other evolutionary forces, for which the analogy with Newtonian mechanics provides no clear guidance.

Let us now consider potential points of positive analogy between evolutionary forces and Newtonian forces. There are (at least) two different ways in which they may be analogous:

1. Evolutionary forces are like Newtonian forces in the way that they are used to construct mathematical models of the evolution of a system in time.
2. Evolutionary forces are like Newtonian forces in being causes of the temporal evolution of the system.

Claim 2 is the primary source of disagreement between defenders of the dynamical and statistical interpretations of evolutionary theory. Claim 1 is, in a certain sense, easier to assess. That is because it can be evaluated by examining the practice of evolutionary biology and Newtonian mechanics, without having to unearth the metaphysical commitments that underlie the practice. This makes possible an argument from analogy that nicely fits Hesse's framework. A defender of the dynamical interpretation could first establish 1, thus establishing a positive analogy between

5. On the other hand, as several commentators have pointed out, the climate does create a selective pressure *against* the PGI-4 allele. More generally, any selective pressure for some trait must be a selective pressure against one or more alternatives.

6. As Kenny Easwaran and others have pointed out to us, friction and elastic forces, which we discuss in some detail below, actually emerge from the aggregate statistical behavior of more elementary forces in certain kinds of system. However, in macroscopic physical systems, the numbers are so great that no substantial deviation from the expected value can be anticipated.

7. Charles Pence (2012) examines the analogy between drift and Brownian motion and its implications for the forces debate.

evolutionary and Newtonian forces. 2 would remain part of the neutral analogy. Then, one could argue for extending the positive analogy from 1 to 2. Like any argument from analogy, this argument would be highly defeasible and could be undermined by a more careful examination of the metaphysical commitments of evolutionary theory. While no author has framed the argument in quite this form, we take this kind of argument to be implicit in the work of many defenders of the dynamical view. For example, Rice (2004: 130–131) treats selection and mutation as population level directional processes. Then, he says, “[w]e can thus represent their effects in terms of *vector fields* over the space of allele frequencies. . . . Combining these processes becomes easy, in that, for any value of p we can simply add together the two vector fields to get the joint effects of the two processes. In this sense, selection and mutation behave like forces in physics.”

In response, it is open to the defender of the statistical interpretation to challenge 1. Of the four specific arguments from Matthen and Ariew (2002; 2009) that we discuss below, three strike us as being directed primarily against 1. The fourth (the *tertium quid* argument) seems to directly challenge 2.

Before examining these arguments, we wish to briefly mention a possible strategy for blocking the inference from 1 to 2 that has not been explored.⁸ Defenders of the statistical view have assumed that component forces in Newtonian mechanics are causes of motion,⁹ and we will follow suit.¹⁰ But there are a number of subtle and interesting issues about how to apportion causal responsibility among component forces, the sources of such forces, and resultant (or net) forces in Newtonian mechanics.¹¹ It is possible that there is a defensible view about the causal status of Newtonian forces that a defender of the statistical interpretation would find to be an attractive analogue. In this case, the analogy between evolutionary and Newtonian forces may even bolster the statistical interpretation. While we will not explore this possibility here, our arguments will not foreclose this pos-

8. We would like to thank an anonymous referee for prompting this discussion.

9. For one example, Matthen and Ariew (2002: 59) write that “component forces act independently of one another. . . . This independence condition for component causation, which we regard as indispensable to the Newtonian apparatus of resolved force, fails in the evolutionary case. . . . [I]f Sober’s conception of evolutionary fitness is right . . . the . . . causes of evolution [should] add up to a resultant force. If the analogy with Newtonian mechanics is to be maintained, these components should, despite such summation, retain their separate causal influences.”

10. More precisely, we will assume that a force acting on a body during the open time interval (t, t') is a cause of its position and velocity at time t' and later. It is more problematic to say that a force acting at time t is a cause of the instantaneous acceleration at t (as related in Newton’s second law). We remain neutral toward that claim.

11. See for example Jammer (1957), Creary (1981), Cartwright (1983: Chapter 3), Forster (1988), and Wilson (2007; 2009).

sibility.¹² Indeed, a careful examination of the analogy between evolutionary and Newtonian forces of the sort we hope to provide would be a necessary precursor to developing such an argument.

While conflating a negative analogy with a positive analogy is one kind of error, there is another kind of error whose possibility is less immediately apparent. When the target and model systems have complex structures, as do Newtonian mechanics and evolutionary theory, it is not always enough to say which parts of each system belong to the positive analogy. For this can still leave it undetermined which elements of the target system are analogous to which elements of the model system. For example, even if we grant that evolutionary forces are analogous to forces in Newtonian mechanics, it may turn out that a particular evolutionary force, such as natural selection, is more closely analogous to some specific Newtonian force than to others. We will argue that this is in fact the case and that the internal structure of the analogy is a little surprising. If one were asked to name forces in Newtonian mechanics, one would almost certainly start with gravity. Second would probably be electromagnetic forces, such as the force of electrostatic attraction described in Coulomb's law. Call these the canonical Newtonian forces. Forces such as friction and elastic forces would come further down the list. Similarly, if asked to name evolutionary forces, natural selection would almost certainly spring to mind first. It is the canonical evolutionary force. Genetic drift would likely come second. Mutation and migration are likely to enter the list only as afterthoughts. We will argue that natural selection is most closely analogous to non-canonical Newtonian forces such as elastic forces, while mutation and migration are more closely analogous to the canonical Newtonian forces such as gravitation. Drift, as we mentioned above, seems closer to Brownian motion than to any force. Thus the analogy between forces in evolutionary theory and Newtonian mechanics exhibits a kind of mismatch, where the canonical forces of one theory are not matched up with the canonical forces of the other. (This is shown schematically in figure 1.)

It is possible that this mismatch may serve some of the needs of defenders of the statistical interpretation of evolutionary theory. For example, in physics, gravity, electromagnetism, and the weak and strong nuclear forces are considered *fundamental* forces; friction and elastic forces are not. These forces arise on the aggregate level from the action of the fundamental forces (especially electromagnetic forces). The situation is a bit tricky, since the details of how these forces arise are not completely understood. Moreover, the explanation will likely take us out of the realm of Newtonian mechanics. It will certainly take us beyond the mechanics taught in a first year university physics course, which is what we take to be the

12. Except to the extent that our discussion of the tertium quid argument precludes certain views about Newtonian forces.

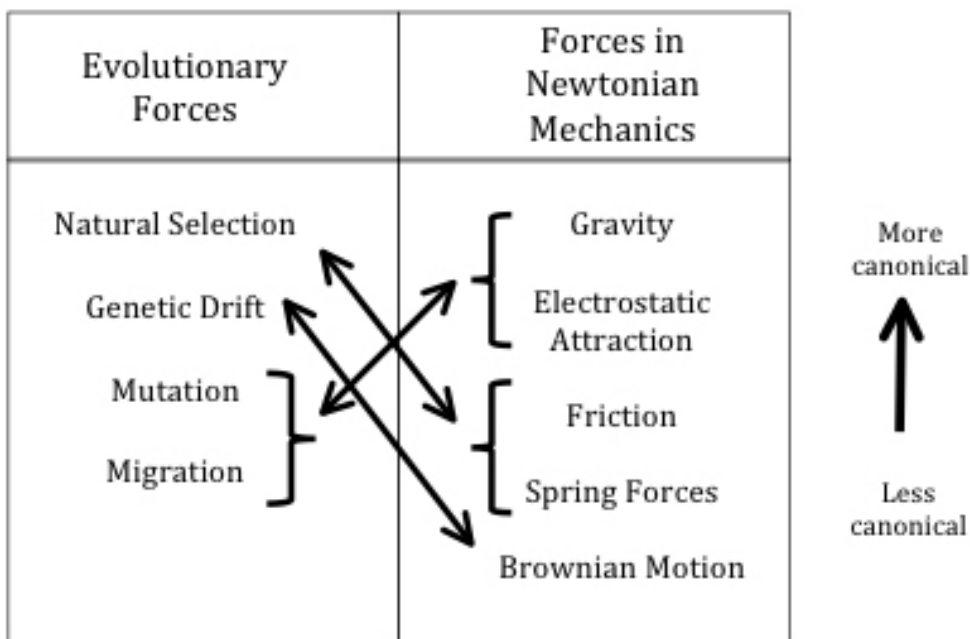


Figure 1. The analogy between evolutionary and Newtonian forces. The more canonical evolutionary forces are most closely analogous to less canonical Newtonian forces, and vice versa.

intended model system for purposes of the analogy with evolutionary biology. So it may be fair to say that from the perspective of elementary Newtonian mechanics, friction and spring forces are basic. But let us put these concerns aside. It would seem that an analogy between natural selection and these non-fundamental forces would provide support for claim 11 above, namely, that natural selection supervenes on the births, deaths, and matings of individual organisms.

It is not clear to us that much mileage can be gotten from this claim (which some proponents of the dynamical interpretation, such as Shapiro and Sober, 2007, accept). One can imagine an argument, perhaps similar to Kim's (1998) well-known argument for the causal inefficacy of mental properties (if non-reductive materialism is true), that supervenient forces such as friction and natural selection are not causes.¹³ But we do not interpret defenders of the statistical interpretation of evolutionary biology to be making any kind of argument that extends to macro-causation generally. Their arguments are specific to evolutionary biology, and hinge on the details of that theory. Moreover, defenders of the statistical interpretation seem happy to talk about certain macro-level causes, such as causes of

13. We would like to thank an anonymous referee for pressing us on this point.

changes in specific populations.¹⁴ But we are open to the possibility that defenders of the statistical interpretation may exploit the analogy between natural selection and non-fundamental forces in Newtonian mechanics to their advantage.

5. Criticisms of the Forces Analogy

We identify four primary arguments offered by Matthen and Ariew (2002; 2009) to claim that natural selection, drift, mutation, migration, and so on are not analogous to Newtonian forces.

1. *Isolability*. In Newtonian mechanics, it makes perfect sense to ask what would happen if a single force were to act on a lone body in isolation. For instance, we can calculate the motion of a body that is subject to a gravitational force, even if it is otherwise in a complete vacuum. By contrast, it makes no sense to ask what would happen if natural selection were acting in isolation. Natural selection can only act in some physical “substrate” (Matthen and Ariew 2002: 68). Such a substrate will include such things as an organism’s means of reproduction, the mechanisms of inheritance, and so on. For example, *heterosis* (when heterozygotes have higher fitness than either homozygote) can only take place in sexually reproducing diploid populations. Even Sober’s (1984) candidate for a zero-force law, the Hardy-Weinberg law, only holds for sexually reproducing diploid populations. This substrate is not just another force whose effect can be independently added.
2. *Source laws*. There are “source laws” for forces, such as Coulomb’s laws, and the law of universal gravitation. These laws provide independent values for component forces. Thus, forces have empirical content beyond what they imply about the acceleration of the body that is acted on (in accordance with the second law). By contrast, the parameters that appear in evolutionary theory, such as fitness coefficients, can only be interpreted in terms of the response of the population. A fitness coefficient represents the expected number of offspring of organisms of a particular type (usually in comparison with other organisms in the population). There are no source laws that tell you, e.g., that whenever an organism has trait X in environment Y, its fitness will be w .
3. *Composition of forces*. Newtonian forces combine according to a simple addition law. To determine the effect of two forces acting together, we can first determine the effect of each force acting alone (which is possible by 2) and

14. For example, Matthen and Ariew (2009: 203) endorse the claim that variation with respect to camouflage in certain moth populations has caused changes in those populations.

add the effects together. This allows us to determine how much of a body's motion is due to one force, and how much is due to another. There is no general rule for how evolutionary "forces" combine. For example, consider an organism that "undertakes parental care, is resistant to malaria, and is somewhat weak but very quick" (Matthen and Ariew 2002: 67). There is no rule for combining these fitness-affecting traits to arrive at a fitness value for the organism.

4. *Tertium quid*. Newtonian forces are a tertium quid. They are causes that appear in a causal chain: A source (such as a massive body) produces a force, which in turn causes motion. These three things are all distinct. By contrast, natural selection is not a tertium quid. It does not exist independently of the traits of organisms in a population, and individual events of birth, death, reproduction, etc.

We will argue that all four of these alleged disanalogies rest on misconceptions about Newtonian forces.

Isolability

We agree that evolutionary forces can only act in some kind of physical substrate. By contrast, one massive body can exert a gravitational force on another even in the absence of other forces.¹⁵ However, it is not true that all Newtonian forces are capable of acting in the absence of other forces. Consider electrostatic forces. It is material bodies that have charges and these material bodies will also have mass and thus exert a gravitational force. If one body exerts an electrostatic force on another, it must also exert a gravitational force on that same body and thus it is impossible for electrostatic forces to act in isolation.

Of course this "impossibility" result depends on the fact that all bodies that have charge also have mass. Perhaps we do not want to build this in to Newtonian mechanics as a conceptual fact. It is at least conceivable that there are massless bodies that do have charges and it is unclear that Newtonian physics rules this out.

But consider the case of friction. Suppose a block is resting on an inclined surface. (See figure 2.) A gravitational force, \mathbf{F}_g , pulls straight down on the block. The surface pushes back against the block with a force that is normal to the surface, \mathbf{F}_n . When added together, these two forces will yield a force that pulls the block down the inclined slope. The force of friction \mathbf{F}_f will oppose this force, impeding the block's motion down the slope, with a maximum magnitude equal to $\mu\mathbf{F}_n$, where μ

15. Not counting the equal and opposite force that the second body exerts on the first. We have already granted that Newton's third law is not directly analogous to anything in evolutionary theory.

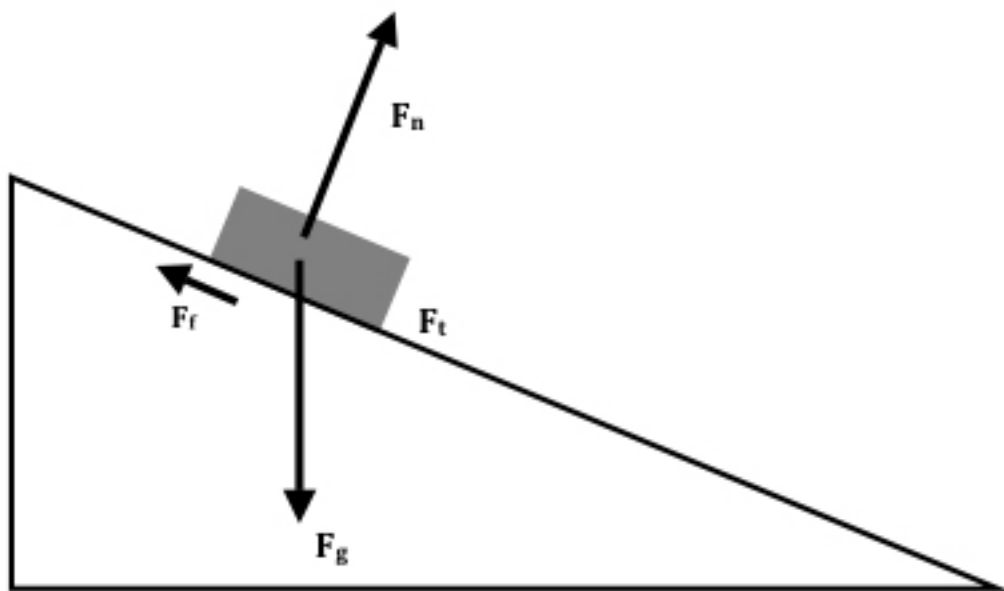


Figure 2. The force of friction opposes the motion of a block along an inclined surface.

is the coefficient of friction between the block and plane.¹⁶ The only law in Newtonian mechanics that tells us how friction works tells us that there is a force due to friction exactly when there is a normal force acting on the body (and, if the body is not already in motion, some force tending to move the body along the surface). Thus friction forces never operate alone: they always require at least a normal force to be present. This undermines the claim of Matthen and Ariew that Newtonian forces (unlike evolutionary forces) can always be considered in isolation.

There is another sense in which Newtonian forces require a substrate. In Newtonian mechanics, all forces operate against a substrate of space and time. For Newton, this was simply Euclidean absolute space plus absolute time. But we know now that there are other possibilities. Newton's first law can be understood as telling us that when no forces act on a body, it follows a geodesic (either of space, or of the underlying space-time). In a non-Euclidean geometry, for example, two particles can be traveling in parallel, with identical uniform velocities, and nonetheless approach and recede from one another. This is due to the metrical structure of the space, and not due to any forces acting on the bodies. In general relativity, a body

16. The story is a bit more complicated. There are separate coefficients for *static friction*, which must be overcome in order for the block to start moving, and *kinetic friction*, which applies once the block is sliding down the surface. The coefficient of static friction is generally larger.

with no forces acting on it follows a geodesic in a four-dimensional space-time whose metric has a Lorentzian signature. In this framework, the earth undergoes uniform motion in its orbit about the sun. Any force that acts on a body will then cause it to deviate from the geodesic. Indeed, the notion of *acceleration* only makes sense in the context of a space-time with a certain amount of metrical structure.

As Poincaré and Reichenbach have taught us, it is sometimes possible to absorb forces into the space-time structure, or to pull them out of it. For example, in Newtonian mechanics, gravity is a force. But it is possible to formulate an empirically equivalent physical theory in which gravity is incorporated into the space-time structure, much as it is in general relativity.

Newtonian physics (at least in its standard formulation) also requires a reference frame. Normally the laws of Newtonian mechanics are taken to describe the behavior of bodies in an inertial reference frame. But it is sometimes convenient to use different reference frames, and these can give rise to fictitious forces. For instance, in the coordinate frame of a rotating disk, there will be centrifugal “forces” pulling bodies toward the edge of the disk. In actuality, these forces result from the tendency of bodies to continue moving in straight lines (which appear to be accelerated trajectories in the rotating frame). On the surface of a rotating sphere (such as the earth), there will be Coriolis forces, and so on.

We suspect that in evolutionary biology, there may be similar cases where there is some flexibility as to whether something is treated as a force, or whether it is incorporated into the substrate in which other forces act. For example, Sober states directly that the typical way of presenting evolutionary theory takes evolution to occur with the background of the Mendelian inheritance system. This means that various kinds of genotypic features of a population (like the percentage of heterozygotes) can change due to the Mendelian process, but evolutionary theory does not record this change as the results of any forces. On the other hand, features such as genetic linkage are treated as forces. Sober explicitly compares this to gravitation in general relativity (Sober 1984: 35–36).

Brandon (2006) and McShea and Brandon (2010) argue that genetic drift is not a force, and that its operation should be incorporated into the zero-force law. In effect, they claim that drift is kinematic (like inertia) rather than dynamic (like the response to a genuine force). We suspect that this is a case where there is some flexibility about whether to treat drift as a force, or to incorporate it into the operation of the substrate.¹⁷

17. Indeed, McShea and Brandon (2010) suggest that it is a matter of convention how causes are partitioned into forces. Maudlin (2004) suggests something similar. Thanks to an anonymous referee for pointing this out.

Source Laws

In Newtonian mechanics, there are (at least) two different kinds of laws in which forces appear. (We put aside Newton's third law, which does not have an obvious evolutionary analogue.) First, there are *source laws*, which specify the conditions under which certain kinds of component forces act on a body. Canonical examples include Newton's universal law of gravitation and Coulomb's law of electrostatic forces. Newton's law tells us that if we have two massive bodies with masses m_1 and m_2 , separated by distance r , the force of gravity acting on each body is $\mathbf{F}_g = Gm_1m_2/r^2$, directed inward along the line connecting the two bodies. (This assumes that the bodies are small compared to the distance between them.) G is the gravitational constant. Coulomb's law tells us that if we have two bodies with charges q_1 and q_2 , separated by distance r , the electrostatic force acting on each body is $\mathbf{F}_e = k_e q_1 q_2 / r^2$, where k_e is Coulomb's constant, and the force is directed outward along the line connecting the two bodies (resulting in an inward or attractive force when $q_1 q_2$ is negative). Second, there is the consequence law, Newton's second law, which tells us that $\mathbf{F}_{\text{net}} = m\mathbf{a}$, where \mathbf{F}_{net} is the net force acting on a body, m is the body's mass, and \mathbf{a} is the body's (instantaneous) acceleration. This tells us how a body will move in response to all of the forces acting on it.

Source laws give us a means of calculating component forces that is independent of the resulting acceleration. For example, if we wish to model the trajectory of a comet, we can calculate the sun's gravitational force on the comet; we do not need to observe the comet's acceleration and put the gravitational force in "by hand." Similarly, if a body is affected by more than one force (say a gravitational force and an electrostatic force), we can calculate the separate component forces, even though the acceleration can only tell us about the value of the net force. Even if the forces acting on a body add up to zero, so that the body does not accelerate at all, we can use the source laws to calculate the individual component forces acting on the body.

It is natural to assume that this independent means of epistemic access to Newtonian forces gives us some reason to think that they are real, and that they are distinct from the accelerations that they produce. Both of these conditions are prerequisites for Newtonian forces to be *causes* of the motions of bodies.¹⁸ If evolutionary forces do not have source laws providing analogously independent means of epistemic access, this would be an important disanalogy that would bear on the causal status of evolutionary forces.

18. We would like to thank Sam Baron for pressing us on the connection between source laws and causation.

According to Matthen and Ariew, the closest analogues that evolutionary theory provides to the source laws of Newtonian mechanics are qualitative and comparative claims about the reproductive advantages of various traits. General ecological considerations might tell us, for example, that speed would be a beneficial trait in a prey species inhabiting open grasslands; physiology might tell us that anemia would be detrimental; malaria resistance would be beneficial in habitats where malaria is endemic, but would be of little use to a species that lived in the arctic; and so on. But these considerations do not provide the quantitative fitness coefficients that figure in population genetics models. The only way to determine fitness coefficients is to observe the actual number of offspring of different organisms. Matthen and Ariew write that

the quantification of fitness in the laws of population genetics is conceptually independent of their occurrence in source laws in a way not paralleled in the Newtonian treatment of force. The overall fitness values demanded by consequence laws [of population genetics] must be estimated statistically, that is, by looking at actual values for number of offspring, and using these actual values to estimate expected values and other statistical quantities. (Matthen and Ariew 2002: 67)

Matthen and Ariew infer from this that fitness coefficients are not quantitative measures of causes of evolutionary change but only estimates of the resulting change.

A more careful examination of both Newtonian mechanics and evolution, however, reveals that both theories include a heterogeneous assortment of forces. Some Newtonian forces conform more closely to Matthen and Ariew's characterization of evolutionary forces, and vice versa.

Gravitational forces and electrostatic forces have source laws essentially as Matthen and Ariew describe. In particular, they have source laws with the following two characteristics:

- (i) The source laws tell us when these forces will be present. Newton's law of universal gravitation tells that a gravitational force will act on a massive body whenever one or more further massive bodies are present. Coulomb's law tells us that an electrostatic force will act on a charged body whenever one or more further charges are present.
- (ii) These source laws tell us how to compute the magnitude and direction of the component forces, in terms of the properties of the sources (their masses and distances, in the case of gravity, or their charges and distances, in the case of electrostatics). The magnitude and direction of these component forces can be calculated without performing any measurements on the

system under investigation. The values of the gravitational and Coulomb constants must be determined empirically (a point made by Brandon and Ramsey 2007), but once they have been determined with a desired degree of precision, the corresponding laws can be applied to new systems without the need for further measurements on those systems.

To Matthen and Ariew, this indicates that gravitational and electrostatic forces have a reality that is distinct from the accelerations that they ultimately produce. These forces are not just measures of a system's expected response to the presence of masses or charges.

But not all forces in Newtonian mechanics are like this. Consider friction. It has feature (i) described above, but only partially has feature (ii). Recall our example of a block on an inclined surface. (Figure 2.) The source law for friction tells us that the force of friction \mathbf{F}_f will oppose the block's motion down the slope, with a maximum magnitude equal to $\mu\mathbf{F}_n$, where μ is the coefficient of friction between the block and the plane. Here the source law tells us when there will be a force due to friction—when there is a force normal to the surface and either a tangential force or motion due to inertia. And it gives us a formula to compute the size of the force. But nothing in Newtonian mechanics tells us what the coefficient of friction will be. This will depend upon the microstructure of the two surfaces, and has to be discovered empirically, through measurements of this very system or other systems involving blocks and surfaces of similar composition.

Now consider the linear restoring force of a spring. Suppose that a spring with a mass attached is stretched beyond its normal relaxation point. (See figure 3.) If it stretches by distance \mathbf{x} , there will be a restoring force, described by Hooke's law: $\mathbf{F}_r = -k\mathbf{x}$, where k is a *spring constant* specific to this particular spring. This source law does not have either feature (i) or (ii) described above. It does not have feature (i) because nothing in Newtonian mechanics tells us when something behaves as a "spring," aside from Hooke's law itself. That is, nothing in the theory tells us what kinds of objects obey Hooke's law. We know that well-made springs obey Hooke's law, to a good approximation, within a limited range. But it is only through experimentation that we can discover, e.g., that a bungee cord approximately obeys Hooke's law, while the string of cheese that connects your teeth to a pizza slice after you bite it does not. We could define a "spring" to be anything that obeys Hooke's law, but as a criterion for the application of Hooke's law, this is obviously circular. Hooke's law also lacks feature (ii), since nothing in Newtonian mechanics tells us what the value of k will be. This is a particular property of any given spring, and it can only be determined by observing the spring in question, or other springs of similar construction.

The situation in evolutionary theory is similar. Matthen and Ariew are correct that natural selection lacks features (i) and (ii). Considerations from ecology,

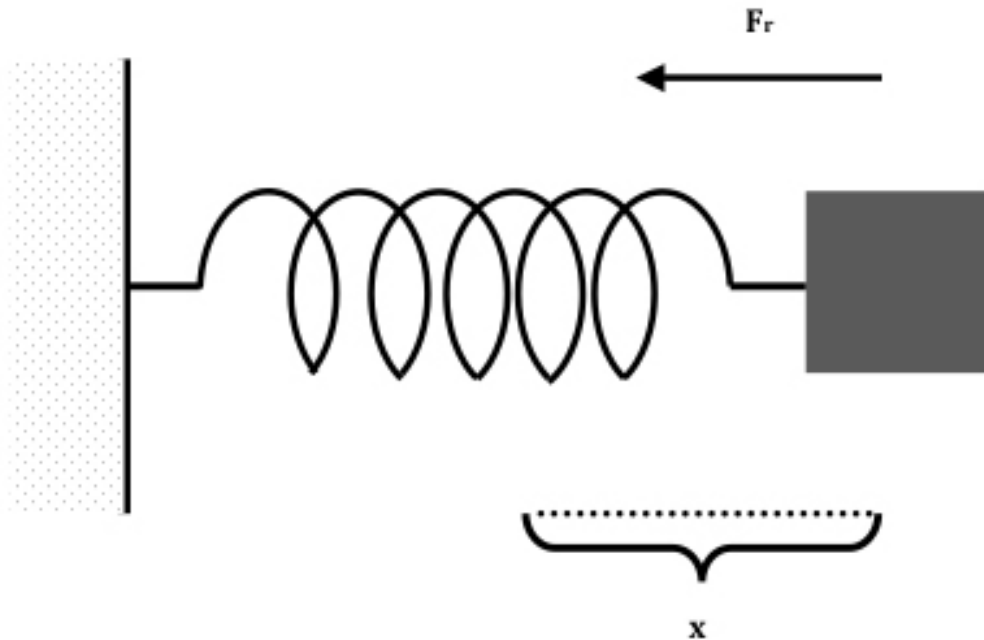


Figure 3. The restoring force in a stretched spring.

physiology, and so on, may give us grounds for thinking that certain traits will be beneficial or detrimental to members of a certain population, but the theory of evolution does not give any definite account of when fitness differences will occur. Nor does it provide formulae for calculating fitness coefficients. The fitnesses of different types of organism in a population typically have to be estimated from observed rates of reproductive success in a population. In this respect, fitness coefficients are like coefficients of friction or spring constants in Newtonian mechanics.

Other evolutionary forces, such as migration and mutation, do have source laws with features (i) and (ii). Migration occurs when individuals immigrate into or emigrate out of a population. One can independently determine how many (and sometimes even which types of) individuals are entering or leaving a population to determine the appropriate parameters to plug into a population genetics model. In a standard model, we assume that migrants are random members of the relevant population. Thus if p_1 is the initial frequency of A in population 1, p_2 the frequency in population 2, and m_{12} the proportion of population 1 recently arrived from population 2 (called the *migration rate*), then the frequency of A in population 1 in the next generation will be $p' = (1 - m_{12}) p_1 + m_{12} p_2$. These parameters do not have to be estimated by observing the response of the population to migration.

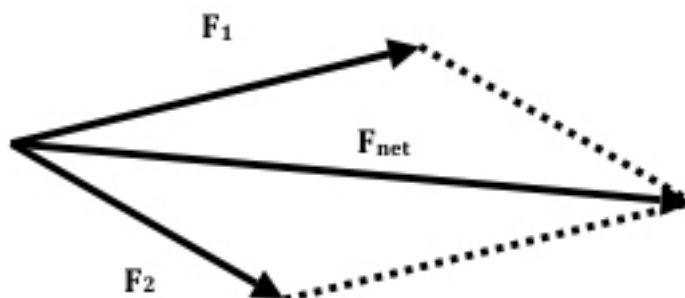


Figure 4. The vector addition rule for forces.

They directly represent these rates of migration, and their numerical values have a clear interpretation that is independent of the expected response of the population. Similarly, mutation rates represent the rates at which mutations occur during meiosis. These can be measured independently of the effects of such mutations on a population and have a clear meaning that is independent of the expected response of the population to mutation pressure.

Composition of Forces

In Newtonian mechanics, forces compose according to the familiar vector addition rule. Suppose that two forces, \mathbf{F}_1 and \mathbf{F}_2 , are acting on a body at a specific time t . (See figure 4.) Then the total force acting on the body at t , \mathbf{F}_{net} , will be the vector sum of the component forces—the result of aligning the vectors ‘tip to tail’. Working in reverse, we can decompose the total force into the two component forces, and specify the contribution of each component force to the total force. Moreover, a component force makes the same contribution to the total force regardless of which other component forces are present. There are no interaction effects among Newtonian forces.

Matthen and Ariew describe the composition of forces this way:

[T]he mathematical device of “resolving” forces by vector addition does not compromise the *separate* operation of “component” forces like gravitation and drag. . . . It makes no difference . . . whether we first combine forces by vector addition and then use Newton’s second law to derive acceleration, or, reversing the order of these operations, first feed the compo-

nent forces into the second law one by one and then use vector addition to combine the separate acceleration vectors that result. . . . Physically, the component forces act independently of one another; there is no mechanism that creates a new force out of them.

This indispensable condition for component causation, which we regard as indispensable to the Newtonian apparatus of resolved force, fails in the evolutionary case. (Matthen and Ariew 2002: 59)

This passage contains a subtle transition that deserves closer examination. Newton's second law, $\mathbf{F}_{\text{net}} = m\mathbf{a}$, relates the total force acting on a body at a given time t with the acceleration of the body *at the very same instant of time* t . Similarly, the vector addition law relates component forces with total forces at the same instant of time. What Matthen and Ariew say about the order of operations is quite correct. In figure 3, we could sum \mathbf{F}_1 and \mathbf{F}_2 to arrive at \mathbf{F}_{net} and then use Newton's second law to calculate the simultaneous acceleration of the body \mathbf{a} . Or, we could apply Newton's second law to \mathbf{F}_1 and \mathbf{F}_2 to arrive at simultaneous component accelerations \mathbf{a}_1 and \mathbf{a}_2 and then add these together to arrive at the same simultaneous acceleration \mathbf{a} .

It is highly misleading, however, to describe this as "component causation." Newton's second law relates simultaneous values of force and acceleration, and it is highly problematic to describe the force \mathbf{F}_{net} as a *cause* of the simultaneous acceleration \mathbf{a} . We will address this issue in greater detail in the next section. This is not to deny that forces cause motions. We take it as unproblematic that the force acting on a body over an interval of time (t_0, t_1) is a cause of the body's position and velocity (*inter alia*) at times $t \geq t_1$. But this kind of causal relation is not governed by anything like a vector addition law. Smith (2010) explains this point in detail. We will give a simple illustration.

Suppose that a small test particle p (perhaps a piece of debris from a comet) is affected by the gravitational force from two massive bodies m_1 and m_2 (perhaps comprising a binary star system). At time $t = 0$, the three bodies have initial velocities \mathbf{v}_p , \mathbf{v}_1 , and \mathbf{v}_2 , respectively. (See figure 5.)

Suppose, first, that only m_1 had been present. (See figure 6.) After a certain amount of time, $t = T$, m_1 would have moved. p also would have moved. Due to the gravitational force of m_1 , the trajectory t_p of p would be deflected from the trajectory t_v that it would have followed if it had continued traveling with uniform velocity \mathbf{v} . The displacement vector d_p may be thought of as measuring the effect of m_1 's gravitational attraction on the trajectory of p . Based on the new positions of both p and m_1 , p will be subject to a gravitational force \mathbf{F}_1 at time $t = T$.

Now, let us return to the case where both m_1 and m_2 are present (figure 7). Because of the gravitational influence of m_2 , both m_1 and p will occupy *different*

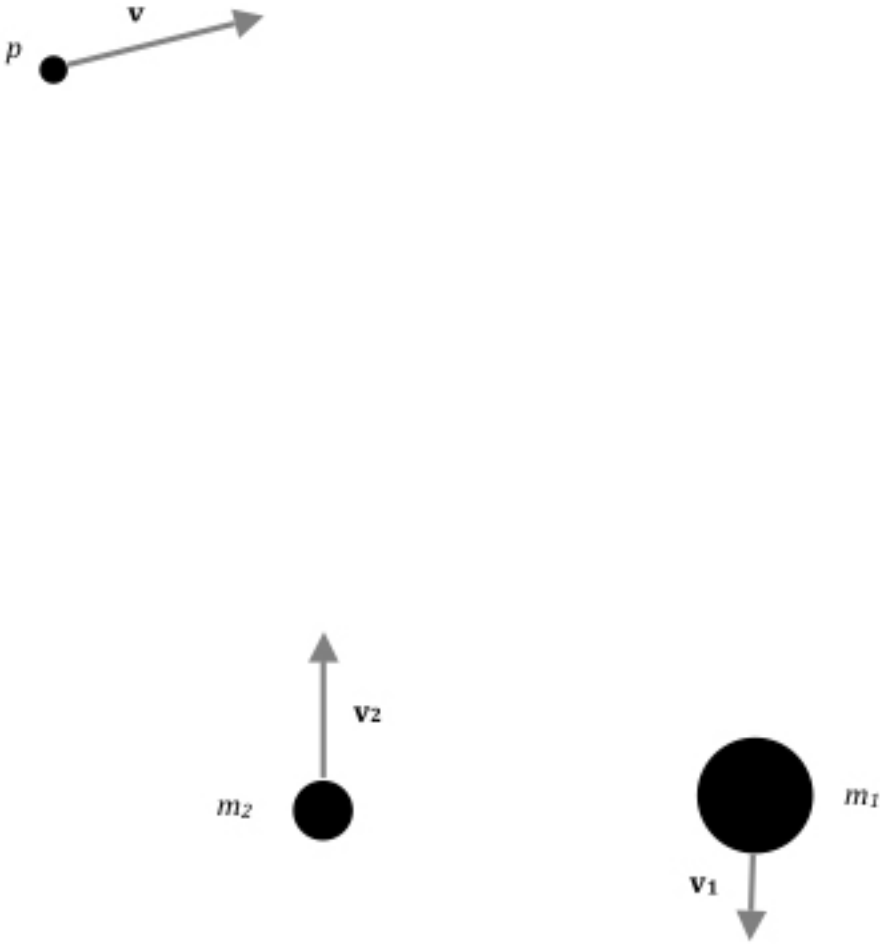


Figure 5. A test particle in the vicinity of two massive bodies.

positions after the same amount of elapsed time. As a result, the component force due to m_1 will be *different* from what it was at the same time in the previous case. This will be the case for every point in the particle's trajectory t_p' , except for the starting position at $t = 0$. Exactly analogous points apply, *mutatis mutandis*, to the gravitational force due to m_2 .

When both m_1 and m_2 are present, then at every point in the particle's trajectory, the component force \mathbf{F}_1' due to m_1 is different from what it would have been if only m_1 had been present, and the component force \mathbf{F}_2' due to m_2 is different from what it would have been if only m_2 had been present. Thus there is absolutely no reason to think that the total displacement d_p' that would result would simply be

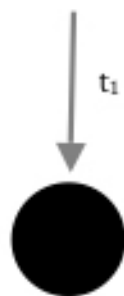
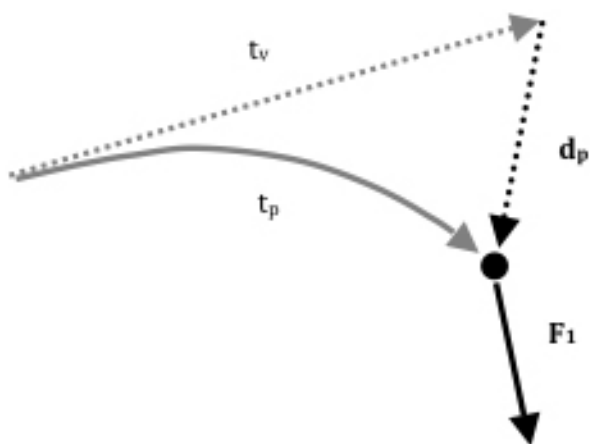


Figure 6. The trajectory of the particle and the gravitational force acting on the particle if only one of the bodies were present.

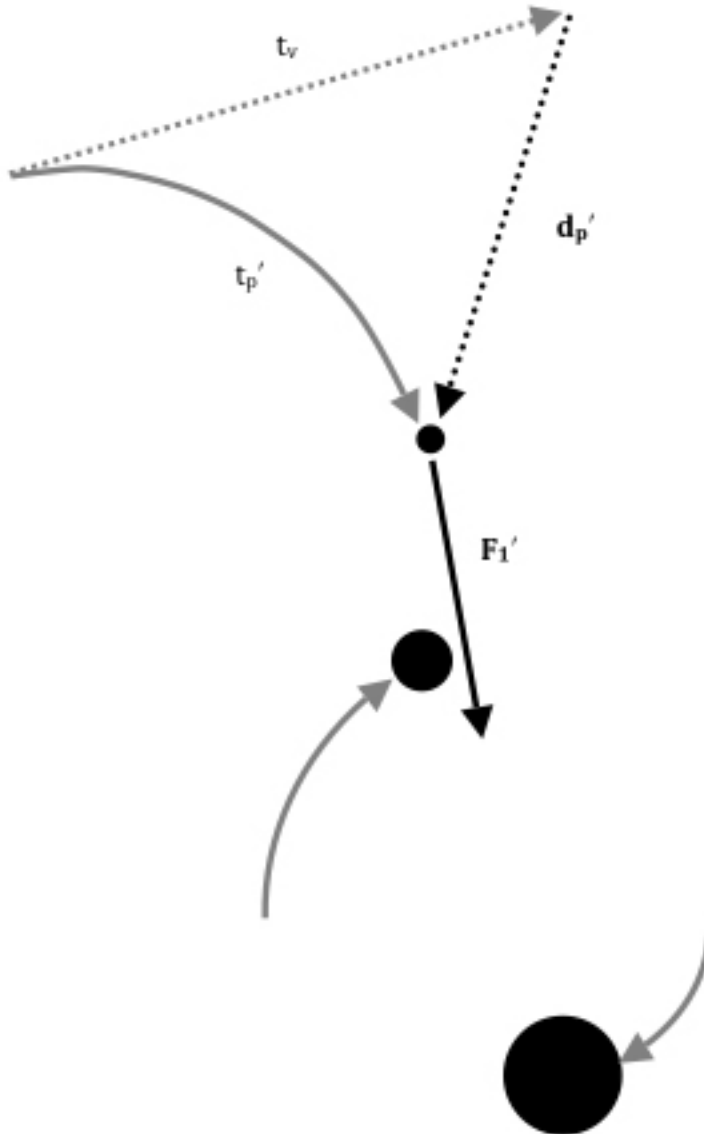


Figure 7. The trajectory of the particle and the gravitational force acting on the particle, with both bodies present.

the sum of the displacement that would have occurred if only m_1 had been present, and the displacement that would have occurred if only m_2 had been present. There is no simple additive law for the *effects* of forces.

Similarly, there is no simple decomposition of the displacement d_p' into parts caused by the gravitational attraction of each mass. At time $t = T$, and at any other time in the trajectory of p , we can decompose the total force acting on p into the two component forces: one due to m_1 , and one due to m_2 . We can even decompose the displacement d_p' into parts due to the instantaneous component forces from m_1 , and the instantaneous component forces from m_2 . But this will not in any meaningful way be a decomposition of the displacement into parts caused by the gravitational forces of m_1 and m_2 . That is because the instantaneous component force due to m_1 at a given time T depends on the positions of p and m_1 , and these have in turn been influenced by the gravitational effects of m_2 on both m_1 and p , and vice versa. *Each* component force reflects the earlier gravitational effects of *both* masses.

The punch line is that insofar as Newtonian forces obey a vector addition law (namely with respect to instantaneous forces and acceleration), they are not unproblematically conceived as causes; and insofar as forces are unproblematically conceived as causes (of *later* positions and velocities) they do not obey a vector addition law. This ought to make us suspicious of the claim that the vector addition law is central to the status of Newtonian forces as causes.

Now let us consider the case of evolutionary forces. We saw the earlier example in which selection and mutation combine in something like an additive way. Brandon and Ramsey (2007) argue that evolutionary forces often do combine additively. For example, they claim that we can find the resulting change in gene frequencies in a population due to selection, mutation and migration by simply adding them up.

Start with a model in which the frequency of an allele A changes from p_1 to $p_2 = w_A p_1$ due to natural selection (where w_A is the relative fitness of A). Now Brandon and Ramsey claim:

Given this very simple model we can easily add the effects of migration and mutation (where μ is the mutation rate from A to a , ν is the mutation rate from a to A , and m_{1A} is the rate of loss of A due to emigration, m_{2A} the gain in A due to immigration, m_{1a} the rate of loss of a due to emigration, and m_{2a} the rate of gain of a due to immigration). (2007: 71)

This results in the following addition:

$$p_2 = w_A p_1 + p_1(1 - \mu) + (1 - p_1) \nu - m_{1A} + m_{2A}$$

$$q_2 = w_a q_1 + q_1(1 - v) + (1 - q_1) \mu - m_{1a} + m_{2a}$$

Brandon and Ramsey are correct that this kind of simple addition is quite common in evolutionary modeling. But this presentation is misleading in several respects.

First, population genetics tracks the *relative frequencies* of alleles, not their absolute frequencies. Hence, after calculating p_2 and q_2 as above, there is a further step of re-normalizing by dividing by $p_2 + q_2$. As a result, the contributions will not be strictly additive. But additivity per se is not really the issue here. The real issue is whether the contributions of selection, migration, and mutation are *independent*. This means, e.g., that the contribution of migration is the same, regardless of the extent of the contribution due to selection and mutation, and that the effect of the three forces working in combination can be calculated from the contribution of the individual forces. This will be true whether the rule for calculating the joint effect is “add the individual contributions together,” or whether it is “add the individual contributions together and then re-normalize.”

A more serious problem with Brandon and Ramsey’s presentation is that it obscures a sensitivity to both time and frequencies. Matthen and Ariew (2009) raise the following objection to Brandon and Ramsey’s example:

Suppose that the rates of mutation, migration, and selection were dependent on one another. Then we couldn’t calculate net change in the simple way that these authors suggest. . . . For as migration occurred, the mutation rate would also be changing. To calculate net change, therefore, we would need to know how mutation varied as a function of migration, and vice versa—and of course we would need the same quantities for selection as well. Here too, combined change under selection, migration, and mutation is not a function of change under selection alone, migration alone, and mutation alone (219).

There are two different ways to interpret the claim “as migration occurred, the mutation rate would also be changing” and others like it. In Brandon and Ramsey’s example, the coefficients μ and v do not represent the *absolute* rates at which parents with allele A produce gametes with allele a , and vice versa, but the *proportional* rates. That is, μ is the *proportion* of parents with allele A that produce gametes with allele a (and similarly for v). It would be very strange indeed if these coefficients were affected by migration or selection. Indeed, the principle that mutations are not *directed* amounts to the claim that mutation rates are not influenced by selection pressures. Matthen and Ariew are certainly correct that *if* μ and v were influenced by migration, the contributions of the different forces would not be additive. But there is absolutely no reason to think that mutation and migration rates would be interdependent in this way.

A more plausible reading of Matthen and Ariew's claim is that the *absolute* rate of mutation from A to a is dependent upon migration and selection in the following sense: The absolute mutation rate in a given generation depends upon the relative frequency of A and a in the parental generation, and this in turn has been influenced by the action of selection and migration. This claim is absolutely correct, and Brandon and Ramsey's presentation obscures this somewhat. First, they present the emigration rates m_{1A} and m_{1a} as constants, but it would be very surprising if these rates did not depend upon the frequency of A and a in the population. Second, Brandon and Ramsey's model represents events that take place over the course of a generation. Let us suppose that p_1 and q_1 are the frequencies of A and a in a population of adult organisms that are about to mate. During meiosis, mutation occurs, and we will have a slightly different distribution of A and a among the gametes produced. Now selection occurs and changes the frequencies again. To calculate the effect of selection, we have to do our calculation using the post-mutation frequencies. Finally, individuals migrate into and out of the population. The number of individuals of types A and a who emigrate from the population will then be determined by the post-selection frequencies of A and a .

If this is what Matthen and Ariew are claiming, then they are entirely correct. How selection for or against an allele A will affect a population depends upon the current frequency of A in the population. The frequency of A in the population, in turn, has been affected by the past action of mutation and migration. Thus if we accumulate the effects of selection, mutation, and migration over many generations, it will be impossible to disentangle the individual effects of selection, mutation, and migration.

But this is *exactly analogous* to the situation in Newtonian mechanics. In the evolutionary case, the effect of one evolutionary force acting at a given time depends upon the frequencies of various alleles in the population, and this in turn depends upon the past action of other evolutionary forces. In Newtonian mechanics, the effect of one component force acting at a given time depends upon the positions of various bodies, and these, in turn, depend upon the past action of other forces. And in both the evolutionary and the Newtonian cases, the total effect of multiple forces acting over time (the change in frequency of an allele and the total displacement vector) is not simply a sum of what the effects would have been if each of the forces had been acting alone.

But perhaps Brandon and Ramsey's example is uncharitable in another respect. Their example involves combining different kinds of evolutionary forces. But perhaps what Matthen and Ariew really have in mind is that the different factors that affect *fitness* do not combine in anything like the way Newtonian forces do. For example, they write:

[W]e have no way of calculating whether a given sex-selection strategy interacts with a given parental care strategy, and how the fitness produced by the variants of these strategies combine. This inability to add the “forces” of fitness is even more pronounced when the source laws are in unrelated domains. Suppose a certain species [sic]¹⁹ undertakes parental care, is resistant to malaria, and is somewhat weak but very quick. How do these fitness factors add up? We have no idea at all. (Matthen and Ariew 2002: 67)

This claim seems correct. And at least some kinds of forces in Newtonian mechanics do add up in the way Matthen and Ariew suggest. For example, we can calculate the gravitational forces exerted by each part of a massive body, add them up, and derive the gravitational force exerted by the body as a whole. But not all Newtonian forces work this way. Consider again the case of friction. Suppose that we know the coefficient of friction between a wooden block and a wooden plane. (See figure 1.) Suppose also that we know how the coefficient of friction would change if we were either to cover the block with sandpaper or to coat the slope with engine oil. Newtonian mechanics provides us with no simple rule for how to combine these to calculate the coefficient of friction that would result if we both covered the block with sandpaper and coated the slope with motor oil. Similarly, there is no simple rule for combining the various factors that affect the value of a spring constant.

Tertium Quid

Matthen and Ariew (2009) argue that a Newtonian force is, while selection is not, a *tertium quid*. By *tertium quid* they mean a distinct causal variable that occurs as an intermediate link in a causal chain. For example, a mosquito bite can cause malaria by causing infection with *plasmodium*, the type of parasite that causes malaria. We have a causal chain in which the mosquito bite causes the infection, which in turn causes malaria. The plasmodium infection is an intermediate cause that is distinct from both the mosquito bite and the disease. They write:

Natural selection is a *tertium quid* on Sober’s account, [footnote omitted] an intervening variable that drives the process [of evolution]. The causal diagram in evolution-by-selection would go like this, according to his account:

19. Species is the wrong category here. If all members of the species are like this, the effect on fitness of these traits will be zero. So we assume Matthen and Ariew intended to say that members of some type within a population have these traits.

heritable variation in trait $T \rightarrow$ selection of magnitude proportionate to variance in heritable fitness due to heritable variation in $T \rightarrow$ birth and death of animals \rightarrow evolution

(Matthen and Ariew 2009: 206)

Matthen and Ariew go on to argue that this is not the proper way to understand natural selection. We are certain that Sober would reject this interpretation of his position; indeed Shapiro and Sober (2007: 249 ff.) appear to argue that this is not the right way to think about what it would be for selection to be a cause. In any event, we will simply agree that natural selection is not a *tertium quid* in this sense.

Matthen and Ariew claim that a Newtonian force, by contrast, is a *tertium quid*. They write:

Newton's Law of Gravitation . . . governs a certain interaction between pairs of massive particles. But most physicists think that this interaction is mediated by a *tertium quid*—the force of gravitational attraction. In other words, they hold that

(7) A massive particle P_1 caused another massive particle P_2 to move is true in virtue of

(8) The gravitational attraction exerted by P_1 caused P_2 to move.

Thus, physicists diagnose gravitation in terms of the following causal diagram:

mass of two particles \rightarrow gravitational attraction of magnitude proportionate to product of masses \rightarrow motion

(Matthen and Ariew 2009: 208–209)

The claim is not merely that the gravitational force is logically or conceptually distinct from the masses of the particles. Nor is it merely that one calculates the effect of the masses by calculating the forces. They claim that the masses of the particles *cause* a gravitational force, which in turn *causes* the motion.

Sober (1984: 50, note 38) explicitly rejects this. He says:

What is the relation of a force to its source? In classical physics, it is a mistake to think of a pair of massive objects separated by a given distance as *causing* a gravitational force to come into existence. The theory holds that the force comes into existence simultaneously with the appearance of the massive objects; so, if causes must precede their effects, we shouldn't view the relation as causal.

However, Newtonian mechanics is a notoriously non-local theory, so perhaps we should not rely on simultaneity to rule out a causal relation between the presence of massive objects and the gravitational force.

Matthen and Ariew (2009) suggest that we use Woodward's manipulability test of causation. (They cite Hausman and Woodward 1999, Woodward 2003, and Woodward 2008.²⁰) According to Woodward, a relationship between two variables is causal if it is stable under interventions, and two variables are distinct if it is possible to intervene on (or manipulate) them independently. Within this framework, in order for the causal diagram

mass of two particles → gravitational attraction of magnitude proportion-
ate to product of masses → motion

to be correct, the following must be true: (i) we can intervene on the mass of two particles and get different gravitational forces; and (ii) we can intervene on the gravitational attraction *while leaving the masses (and positions) of the particles unchanged* and get different motions. Matthen and Ariew recognize that the italicized portion of (ii) is what appears to be problematic:

Since the gravitational attraction between two massive particles supervenes on their masses [and positions], one might think that one cannot manipulate gravitational attraction in the manner proposed. The only way to manipulate gravitational attraction is to change the masses that are attracting one another [or their positions]. (Matthen and Ariew 2009: 210)

Matthen and Ariew then appeal to Woodward's account to argue that such an intervention is possible after all. They cite the following passage from Woodward (2008):

Consider . . . the . . . true . . . causal claim . . .

(G) The gravitational attraction of the moon causes the motion of the tides.

Human beings cannot at present alter the attractive force exerted by the moon on the tides (e.g., by altering its orbit). . . . [I]t may well be that there is no physically possible process that will meet the conditions for an intervention on the moon's position with respect to the tides . . . *For example, it may very well be that any possible process that alters the position of the moon by altering the position of some other massive object will*

20. Matthen and Ariew appear to cite the version of Woodward's entry that was originally published in 2001, which appeared in editions of the *Stanford Encyclopedia of Philosophy* that were archived through September 2008. A revised version was published in October 2008.

have an independent impact on the tides in violation of condition (M₂) for an intervention. It is nonetheless arguable we have a principled basis in Newtonian mechanics and gravitational theory themselves for answering questions about what would happen if such a surgical intervention were to occur and that this is enough to vindicate the causal claim (G).

The phrase in italics appears in Woodward, but was omitted (with appropriate ellipses) when cited by Matthen and Ariew. Matthen and Ariew continue:

Woodward proposes, rightly in our view, that “a properly formulated version of a manipulability theory will thus allow us to talk about causal relationships in some contexts in which interventions are not physically possible” (2008).²¹

We believe that it is possible to envisage a “surgical intervention” on gravitation itself. . . . [W]e have a principled basis in Newtonian mechanics for answering questions about what would happen if we (or God) were to surgically intervene on the relationship between mass and gravitational attraction. If we made it, for instance, an inverse-cube relation instead of an inverse-square relation, or changed the gravitational constant, then we would change the gravitational force exerted by the moon without changing the mass of the moon or of the ocean. (Matthen and Ariew 2009: 211)

In fact, however, Matthen and Ariew have completely misinterpreted Woodward. In the passage cited above, Woodward says:

Human beings cannot at present alter the attractive force exerted by the moon on the tides (e.g., by altering its orbit). . . . [I]t may well be that there is no physically possible process that will meet the conditions for an intervention on the moon’s position with respect to the tides.

This makes it clear that Woodward thinks an intervention on “the attractive force exerted by the moon” would just be “altering its orbit” or “an intervention on the moon’s position.” These are presented as specific ways of intervening on the attractive force (another would be intervening on the moon’s mass). Moreover, the impossibility that Woodward is talking about is not the impossibility of, e.g., changing the law of universal gravitation, but rather the impossibility of changing the position of the moon *while satisfying the other conditions for being an*

21. Interestingly, this passage does not appear in the revised version of Woodward’s entry first published in October 2008.

intervention. Suppose that some cause *I* could change the position of the moon. In order for *I* to count as an intervention on the moon's position with respect to the tides, it must meet several conditions, which he labels (*M*₁) to (*M*₄). The second of these is that *I* must not independently affect the tides. It is clear from the italicized passage, omitted from the citation in Matthen and Ariew (2009), that the problem is that it may be impossible to change the moon's position in a way that does not have a direct effect on the tides (perhaps because of the amount of mass-energy required). This is very different from the impossibility of cranking up the strength of gravitation or changing the law of gravitation to an inverse-cube law.

So what would Woodward say about the kind of hypothetical changes Matthen and Ariew describe? Woodward (2003) describes a similar case:

My focus so far has been on explanations that exhibit patterns of counterfactual dependence having to do with what would happen under interventions. . . . [T]here are derivations that are sometimes regarded as explanatory but that exhibit patterns of dependence that are not naturally interpretable in this way. For example, . . . the stability of planetary orbits depends (mathematically) on the dimensionality of the space-time in which they are situated: such orbits are stable in a four-dimensional space-time but would be unstable in a five-dimensional space-time. [Footnote omitted] Does the dimensionality of space-time explain why the planetary orbits are stable? On the one hand, this suggestion fits well with the idea that explanations provide answers to what-if-things-had-been-different questions. . . . [W]e may think of the derivation as telling what would happen if space-time were five-dimensional . . .

One natural way of accommodating these examples is as follows: the common element in many forms of explanation, both causal and non-causal, is that they must answer what-if-things-had-been-different questions. When a theory tells us how *Y* would change under interventions on *X*, we have . . . a *causal* explanation. When a theory or derivation answers a what-if-things-had-been-different question but we cannot interpret this as an answer to a question about what would happen under an intervention, we may have a noncausal explanation of some sort. This accords with intuition: it seems clear that the dependence of stability on dimensionality . . . is not any sort of causal dependence. (220–221)

Woodward's example about changing the dimensionality of space-time is actually very close to Matthen and Ariew's example about changing the inverse-square law to an inverse-cube law. Many phenomena in physics obey an inverse-square law.

Consider a brief pulse of sound. As the sound travels outward from its source, the energy occupies a spherical shell. The intensity of the sound will be inversely proportional to the surface area of the sphere (the energy from the source is now spread over the surface of the sphere). Hence we have an inverse-square law. But if space had four dimensions, we would expect these phenomena to obey an inverse-cube law. So adding a dimension to space-time is very much like changing the inverse-square law to an inverse-cube law.

So we can sensibly ask what would happen if gravity obeyed an inverse-cube law (it would not be pretty). And this might provide an explanation of some sort. But this would not be an intervention on the strength of gravity, and it would not tell us about any kind of causal relation.

We conclude that there is nothing in Woodward's account of causation to support Matthen and Ariew's contention that a Newtonian force is a *tertium quid*.²²

6. The Forces Analogy

We conclude that none of Matthen and Ariew's arguments succeed in showing a disanalogy between evolutionary forces and Newtonian forces. In fact, we think the analogy is a good one. However, the analogy succeeds, in part, because Newtonian forces and evolutionary forces are both heterogeneous. Gravity is very different from friction, and natural selection is very different from migration. Thus, to say that evolutionary forces are like Newtonian forces tells us comparatively little about any particular evolutionary force, such as natural selection. If evolutionary forces are like Newtonian forces, that implies that natural selection must be like some Newtonian force or other; but it does not imply that natural selection is like gravity, or that it is like friction. In fact, our discussion suggests that it is more like friction than gravity. We suspect that this is one reason why critics of the dynamical interpretation have mistakenly rejected the forces analogy.

Acknowledgments

For helpful comments and discussions, we would like to thank two anonymous referees and an editor at *Ergo* as well as André Ariew, Sam Baron, Mark Colyvan, Kenny Easwaran, Luke Glynn, Mohan Matthen, Peter Menzies, Roberta Millstein, Elliott Sober, Chris Stephens, James Woodward, and audience members at the University of British Columbia, Texas Tech University, the American Philosophical

22. We would like to thank James Woodward for helpful comments on this section.

Association (Pacific Division), the Society for Exact Philosophy, and the University of Sydney.

References

- Abrams, Marshall (2007). How Do Natural Selection and Random Drift Interact? *Philosophy of Science*, 74, 666–679. <http://dx.doi.org/10.1086/525612>
- Barrett, Martin, Hayley Clatterbuck, Michael Goldsby, Casey Helgeson, Brian McLoone, Trevor Pearce, Elliott Sober, Reuben Stern, and Naftali Weinberger (2012). Puzzles for ZFEL, McShea and Brandon's Zero Force Evolutionary Law. *Biology and Philosophy*, 27(5), 723–735. <http://dx.doi.org/10.1007/s10539-012-9321-7>
- Brandon, Robert (2006). The Principle of Drift: Biology's First Law. *Journal of Philosophy*, 103, 319–335.
- Brandon, Robert, and Grant Ramsey (2007). What's Wrong with the Emergentist Statistical Interpretation of Natural Selection and Random Drift? In David Hull and Michael Ruse (Eds.), *Cambridge Companion to the Philosophy of Biology* (66–84). Cambridge University Press. <http://dx.doi.org/10.1017/CCOL9780521851282.004>
- Cartwright, Nancy (1983). *How the Laws of Physics Lie*. Oxford University Press. <http://dx.doi.org/10.1093/0198247044.001.0001>
- Creary, L. (1981). Causal Explanation and the Reality of Natural Component Forces. *Pacific Philosophical Quarterly*, 62, 148–157.
- Dowe, Phil (2000). *Physical Causation*. Cambridge University Press. <http://dx.doi.org/10.1017/CBO9780511570650>
- Filler, Joshua (2009). Newtonian Forces and Evolutionary Biology: A Problem and Solution for Extending the Force Interpretation. *Philosophy of Science*, 76(5), 774–783.
- Forster, Malcolm R. (1988). Unification, Explanation, and the Composition of Causes in Newtonian Mechanics. *Studies in History and Philosophy of Science*, 19, 55–101. [http://dx.doi.org/10.1016/0039-3681\(88\)90020-9](http://dx.doi.org/10.1016/0039-3681(88)90020-9)
- Hausman, Daniel, and James Woodward (1999). Independence, Invariance, and the Causal Markov Condition. *British Journal for the Philosophy of Science*, 50, 521–583. <http://dx.doi.org/10.1093/bjps/50.4.521>
- Hesse, Mary (1966). *Models and Analogies in Science* (Rev. ed.). University of Notre Dame Press.
- Jammer, Max (1957). *Concepts of Force: A Study in the Foundations of Dynamics*. Harvard University Press.
- Kim, Jaegwon, (1998). *Mind in a Physical World*. MIT Press.
- Kimura, Motoo (1968). Evolutionary Rate at the Molecular Level. *Nature*, 217, 624–626. <http://dx.doi.org/10.1038/217624a0>
- Kitcher, Philip (1981). Explanatory Unification. *Philosophy of Science*, 408, 507–531. <http://dx.doi.org/10.1086/289019>
- Kitcher, Philip (1989). Explanatory Unification and the Causal Structure of the World. In Philip Kitcher and Wesley Salmon (Eds.), *Scientific Explanation* (410–505). University of Minnesota Press.
- Lewens, Tim (2004). *Organisms and Artifacts: Design in Nature and Elsewhere*. MIT Press.
- Lewens, Tim (2010). The Natures of Selection. *British Journal for the Philosophy of Science*, 61, 313–333. <http://dx.doi.org/10.1093/bjps/axp041>

- Matthen, Mohan, and André Ariew (2002). Two Ways of Thinking about Fitness and Natural Selection. *Journal of Philosophy*, 119, 55–83.
- Matthen, Mohan, and André Ariew (2009). Selection and Causation. *Philosophy of Science*, 76, 201–224. <http://dx.doi.org/10.1086/648102>
- Maudlin, Tim (2004). Causation, Counterfactuals, and the Third Factor. In John Collins, Ned Hall, and L. A. Paul (Eds.), *Causation and Counterfactuals* (419–443). MIT Press.
- McShea, Daniel W., and Robert N. Brandon (2010). *Biology's First Law: The Tendency of Diversity and Complexity to Increase in Evolutionary Systems*. The University of Chicago Press. <http://dx.doi.org/10.7208/chicago/9780226562278.001.0001>
- Millstein, Roberta (2006). Natural Selection as a Population-Level Causal Process. *British Journal for the Philosophy of Science*, 57, 627–653. <http://dx.doi.org/10.1093/bjps/axl025>
- Morton, Newton E., James F. Crow, and H. J. Muller (1956). An Estimate of the Mutational Damage in Man from Data on Consanguineous Marriages. *Proceedings of the National Academy of Sciences USA*, 42, 855–863. <http://dx.doi.org/10.1073/pnas.42.11.855>
- Ohta, Tomoko, and John H. Gillespie (1996). Development of Neutral and Nearly Neutral Theories. *Theoretical Population Biology*, 49, 128–142. <http://dx.doi.org/10.1006/tubi.1996.0007>
- Pence, Charles (2012). It's Okay to Call Genetic Drift a "Force." Manuscript in preparation. Retrieved from <http://philsci-archive.pitt.edu/9256/>
- Rank, N. E. and E. P. Dahlhoff (2002). Allele Frequency Shifts in Response to Climate Change and Physiological Consequences of Allozyme Variation in a Montane Insect. *Evolution*, 56, 2278–2289.
- Reisman, Kenneth, and Patrick Forber (2004). Manipulation and the Causes of Evolution. *Philosophy of Science*, 72, 1113–1123. <http://dx.doi.org/10.1086/508120>
- Rice, Sean H. (2004). *Evolutionary Theory: Mathematical and Conceptual Foundations*. Sinauer Associates.
- Ridley, Mark (1996). *Evolution* (2nd ed.). Blackwell Science.
- Rosenberg, Alexander, and Frederic Bouchard (2005). Matthen and Ariew's Obituary for Fitness: Reports of Its Demise Have Been Greatly Exaggerated. *Biology and Philosophy*, 20, 343–353. <http://dx.doi.org/10.1007/s10539-005-2560-0>
- Salmon, Wesley (1984). *Scientific Explanation and the Causal Structure of the World*. Princeton University Press.
- Shapiro, Larry, and Elliott Sober (2007). Epiphenomenalism: The Do's and Don'ts. In P. Machamer and G. Wolters (Eds.), *Thinking about Causes: From Greek Philosophy to Modern Physics* (235–264). University of Pittsburgh Press.
- Smith, Sheldon (2010). Elementary Classical Mechanics and the Principle of the Composition of Causes. *Synthese*, 173, 353–373. <http://dx.doi.org/10.1007/s11229-008-9442-3>
- Sober, Elliott (1984). *The Nature of Selection: Evolutionary Theory in Philosophical Focus* (2nd ed.). University of Chicago Press.
- Sober, Elliott (2011). A Priori Causal Models of Natural Selection. *Australasian Journal of Philosophy*, 89, 571–589. <http://dx.doi.org/10.1080/00048402.2010.535006>
- Stephens, Christopher (2004). Selection, Drift, and the "Forces" of Evolution. *Philosophy of Science*, 71, 550–570. <http://dx.doi.org/10.1086/423751>
- Stephens, Christopher (2010). Forces and Causes in Evolutionary Theory. *Philosophy of Science*, 77(5), 716–727. <http://dx.doi.org/10.1086/656821>

- Templeton, Alan R. (2006). *Population Genetics and Microevolutionary Theory*. Wiley.
<http://dx.doi.org/10.1002/0470047356>
- Walsh, Denis (2000). Chasing Shadows: Natural Selection and Adaptation. *Studies in the History and Philosophy of Biology and the Biomedical Sciences*, 31, 135–153. [http://dx.doi.org/10.1016/S1369-8486\(99\)00041-2](http://dx.doi.org/10.1016/S1369-8486(99)00041-2)
- Walsh, Denis, Tim Lewens, and André Ariew (2002). The Trials of Life: Natural Selection and Random Drift. *Philosophy of Science*, 69, 452–473. <http://dx.doi.org/10.1086/342454>
- Wilson, Jessica (2007). Newtonian Forces. *British Journal for the Philosophy of Science*, 58, 173–205. <http://dx.doi.org/10.1093/bjps/axm004>
- Wilson, Jessica (2009). The Causal Argument Against Component Forces. *Dialectica*, 63(4), 525–554. <http://dx.doi.org/10.1111/j.1746-8361.2009.01216.x>
- Woodward, James (2003). *Making Things Happen: A Theory of Causal Explanation*. Oxford University Press.
- Woodward, James (2008). Causation and Manipulability. In Edward N. Zalta (Ed.), *The Stanford Encyclopedia of Philosophy* (Winter 2008 ed.). Retrieved from <http://plato.stanford.edu/archives/sum2008/entries/causation-mani/>